Hatching success in brackish water of *Perca fluviatilis* eggs obtained from the western Baltic Sea

by

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Abstract. – Estuaries are important spawning areas for many freshwater and marine fishes. This is also the case for Baltic populations of European perch *Perca fluviatilis*, an important commercial species in most of Europe. There is, however, inconsistency in the literature between the maximum salinity tolerance of the eggs *in vivo*, and the salinities at which some populations spawn *in situ* (7 vs. 9.6‰). In the present study, hatching success of perch was determined *in vivo* for a Danish, western Baltic, brackish water population at salinities of 4, 7, 10 and 12‰. Furthermore, in order to place the population genetically among other European perch populations, individual egg samples were sequenced for a 390 base pair fragment of the mtDNA D-loop region. Hatching occurred at all four salinities, with no statistical differences among treatments. Successful hatching at 12‰ is well above salinities of 7‰, which has previously been the highest reported from *in vivo* studies. This discrepancy is likely to be a result of methodological differences (e.g. different temperature) or perhaps interspecific variability in egg hatching abilities among perch populations. The perch from the present study consisted of a mixture of haplotypes similar to the haplotypes known to dominate in the Central and Western Europe and the Baltic Sea regions. Our results highlight the potential for recruitment of perch in coastal waters in the western Baltic Sea and have implications for both coastal management and aquaculture industry.

Key words
Percidae
Perca fluviatilis
Western Baltic Sea
Brackish water
Egg hatching
Population genetics

Résumé. – Éclosion réussie en eau saumâtre d'œufs de *Perca fluviatilis* de la mer Baltique occidentale.

Les estuaires sont d'importantes zones de ponte pour de nombreux poissons d'eau douce et d'eau de mer. Ceci est aussi le cas pour les populations baltiques de la perche européenne *Perca fluviatilis*, une espèce d'importance commerciale en Europe. Cependant, il y a inconsistance dans la littérature entre la tolérance de salinité maximale des œufs *in vivo* et les salinités auxquelles certaines populations pondent *in situ* (7 vs 9,6‰). Dans l'étude présente, le succès de ponte d'une population de perche danoise d'eau saumâtre de la baltique occidentale a été déterminé *in vivo* à des salinités de 4, 7, 10 et 12‰. De plus, afin de placer génétiquement cette population parmi les autres populations de perche européenne, un fragment de 390 paires de base de la région de la boucle D de l'ADN mitochondrial a été séquencé sur des échantillons individuels d'œufs. La ponte a eu lieu aux quatre salinités testées, sans aucune différence statistique entre les traitements. Le succès de ponte à 12‰ est bien au-dessus de celui qui avait été obtenu à 7‰, salinité précédemment rapportée dans des études *in vivo* comme étant la plus élevée. Cette discordance est probablement le résultat de différences méthodologiques (entre autres, différentes températures) ou encore d'une variabilité interspécifique dans la capacité de ponte parmi les populations de perche. La population de perches de notre étude est un mélange d'haplotypes similaires aux haplotypes dominants dans le centre et l'ouest de l'Europe, ainsi que dans les régions de la mer Baltique. Nos résultats mettent en évidence le potentiel de recrutement des perches dans les eaux côtières de l'ouest de la mer Baltique et ont des implications à la fois pour la gestion des côtes et pour l'aquaculture.

Mangroves, estuaries and other brackish water transition zones between limnic and marine environments are major spawning and nursery areas for fishes (Boehlert and Mundy, 1988). The restricted salinity tolerance, however, in the early life stages of many Atlantic and Eurasian species, such as Atlantic cod *Gadus morhua* (Linnaeus, 1758) (Westin and Nissling, 1991), Atlantic herring *Clupea harengus* (Linnaeus, 1758) (Holliday and Blaxter, 1960), Northern pike *Esox lucius* (Linnaeus, 1758) (Jørgensen *et al*., 2010) and roach *Rutilus rutilus* (Linnaeus, 1758) (Härmä *et al*., 2008), often sets the limits of successful recruitment in brackish waters (Saucier and Baltz, 1993; Planque *et al*., 2007). This is also the case for the European perch *Perca fluviatilis* (Linnaeus, 1758), an important top down regulator in many lake ecosystems (Jeppesen *et al*., 2000), which is also of great socio-economic importance in the Baltic region (Kestemont and Mélard, 2000; Berg, 2012; Lindvig and Ebert, 2012). It is genetically variable, probably a consequence of survival in several refugia during recent ice-ages, giving rise to the modern populations of Europe (Nesbø *et al*., 1999; Olsson *et al*., 2011). The perch is a freshwater fish that also occurs in brackish water at salinities of up to 18‰ (Thorpe, 1977;

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Olsen, 2002). *In vivo* experiments have documented egg hatching in water with salinities up to 7‰ (Klinkhardt and Winkler, 1989; Tibblin *et al*., 2012), and until recently, this was in accordance with observations of spawning sites *in situ* up to 6‰ (Snickars *et al*., 2010; Tibblin *et al*., 2012). This consensus, however, was brought into question by the observation of a perch population in the western Baltic Sea spawning at salinities up to 9.6‰ (Skovrind *et al*., 2013).

The aim of the present study is to test the *in vivo* salinity tolerance of the sea spawning population described by (Skovrind *et al*., 2013) *i.e*. to test whether eggs spawned at high salinities are actually able to hatch. Furthermore, in order to find out if the studied population is genetically unique or a part of a larger biogeographic unit, a part of the mitochondrial D-loop region was sequenced and compared to published knowledge about the overall European perch population structure.

MATERIAL AND METHODS

Study area and sampling procedure

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Fertilized perch *Perca fluviatilis* egg strands (Fig. 1A, B) of brackish water origin were collected on the 8th of May, 2013, from the harbour of Ishøj (ISH), 55°36'32"N, 12°23'10"E (see Skovrind *et al*., 2013 for a detailed description of the location). Individual egg samples (approximately 10 × 10 cm) were transferred to small plastic bags with location water. To stabilize temperature conditions the samples in the plastic bags were kept in a 60 L barrel with location water during transport to Den Blå Planet National Aquarium Denmark, Kastrup, Denmark. The collection and transport was conducted in less than two hours. The temperature at the sampling site was 10°C. The salinity at ISH was measured on site from 4th April to 16th May, 2013, every 10 minutes with a stationary temperature and conductivity meter (Hobo Conductivity logger, model U24-002).

Hatching experiment: procedure and data processing

Within 2 hours of arrival at the aquarium, 32 individual egg strands were reduced to a size of approximately 3 × 3 cm. Egg counting in Image-J (US National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/) showed that the reduced egg strands held between 185 and 415 eggs, of which 97% (SD = ± 2) where fertilized. The reduced egg strands were acutely transferred to 1 L aquaria (Fig. 1C) containing water with salinities of 4, 7, 10 or 12‰ (n = 8 for each treatment). The latter two were well above the earlier stated salinity tolerance of perch eggs (7‰; Klinkhardt and Winkler, 1989), and covered the ecologically relevant salinities (Skovrind *et al*., 2013). The temperature of the water surrounding the egg samples during transport

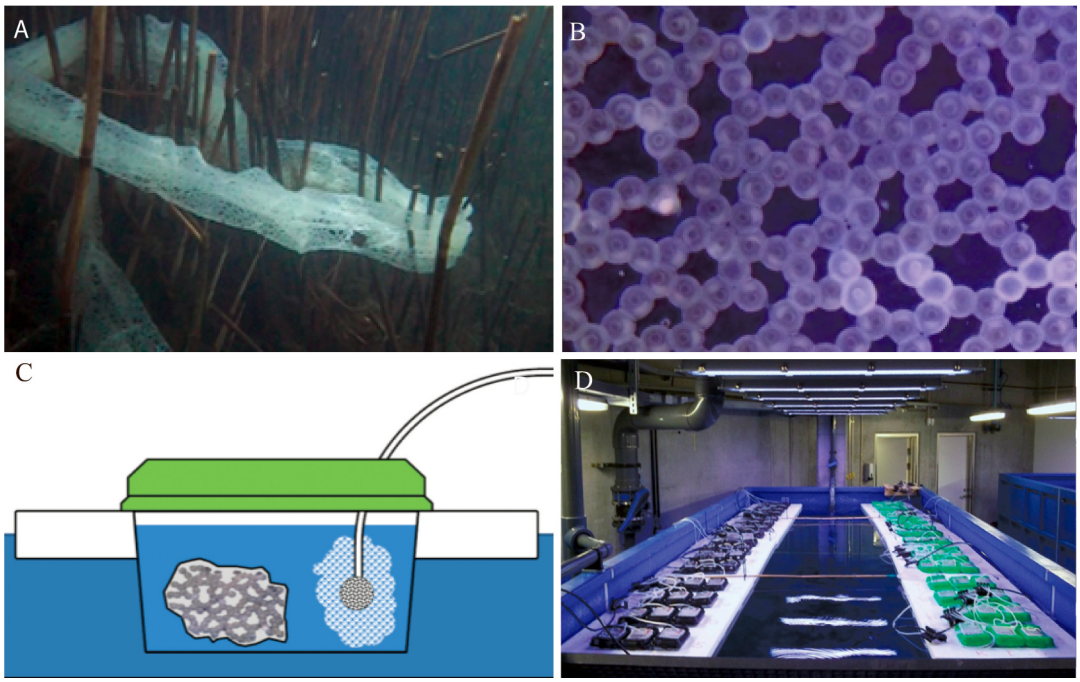

Figure 1. - Experimental setup for the egg hatching study of *Perca fluviatilis*. **A, B**: Fertilized egg strands curled up among reeds in the brackish water of Ishøj Harbour (ISH), 55°36'32"N, 12°23'10"E; **C**: Reduced egg strands in one liter aquaria containing water with salinities of 4, 7, 10 or 12‰ (n = 8 for each treatment); **D**: A total of 32 aquaria (one liter) placed in a 12°C water bath at Den Blå Planet National Aquarium Denmark, in order to stabilize temperature close to the optimal level for incubation of perch eggs.

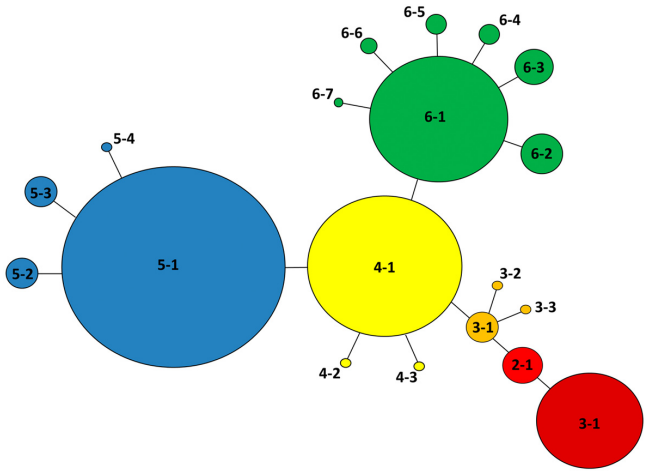

Figure 2. - Haplotype network of perch *Perca fluviatilis* in Europe (n = 707). Each line represents one base pair substitution. Two component numbers (x-y) refers to clade number (x) and haplotype (y). Circle sizes are relative to number of individuals (see text for references).

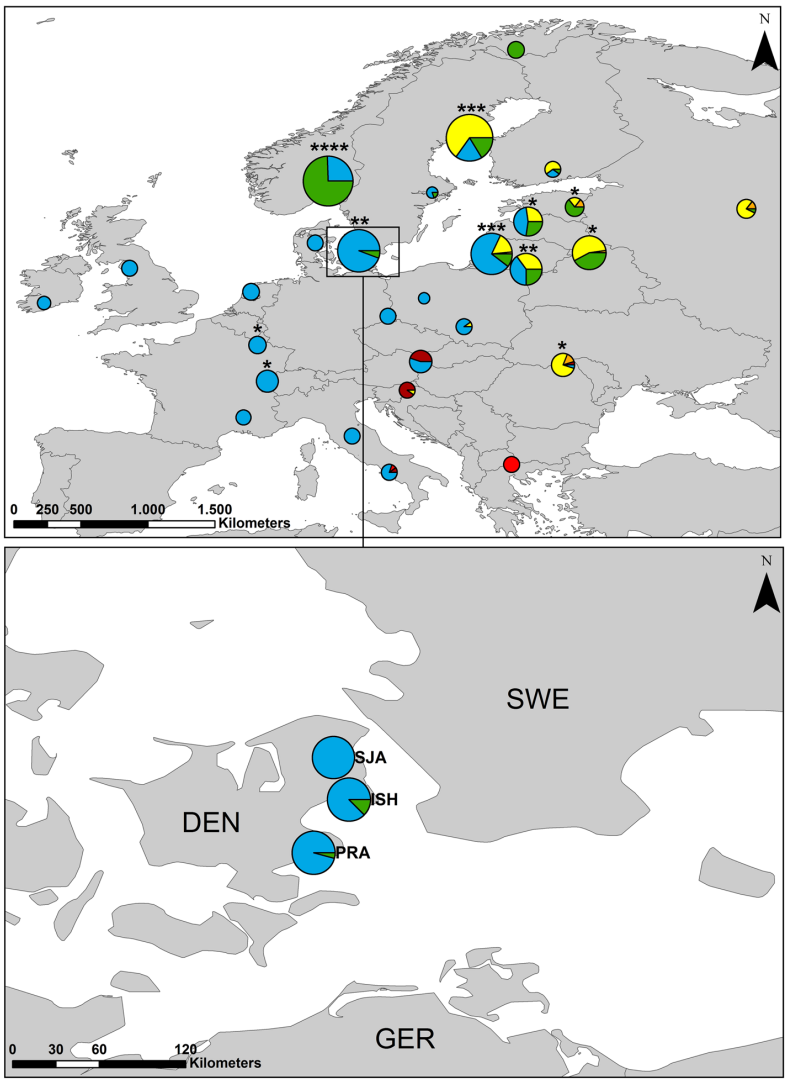

Figure 3. - Distribution of the overall clades of perch *Perca fluviatilis* in Europe, upper map and western Baltic Sea, lower map; Sweden (SWE), Denmark (DEN) and Germany (GER). The pie charts show the relative distribution within a sampling site, and the size of the pie chart the relative sample size. * = fusion of 2 sample sites, ** = fusion of 3 sample sites, *** = fusion of 5 sample sites, **** = fusion of 6 sample sites. Colours are uniform with colours in figure 2.

did not exceed 13°C before the transferal was completed. Each aquarium was aerated and kept in a 12°C water bath (Fig. 1D) to stabilize temperature close to the optimal level for perch eggs incubation (Guma'a, 1978). This temperature was approximately the same as the temperature at the sampling site. The salinity of each treatment was obtained by mixing oceanic seawater with freshwater from the aquarium's water systems. *In vivo* salinities were measured with a digital refractometer (Pocket refractometer PAL-06S from Atago). Approximately 50% of the water was replaced three times a week, where also the salinities were adjusted. Hatching was determined as successful if the embryos evolved eye pigmentation, and hatched into motile larvae. The number of replicates with successful hatching was determined for the whole egg strand and not on the individual egg. This yielded binary data and a Fisher's Exact Tests was employed for statistical, pair wise comparisons between the four treatments.

DNA: sampling, extraction and data processing

A 390 base pair D-loop section of mitochondrial DNA (mtDNA) was sequenced for DNA analyses. DNA was extracted from 24 individual egg strands from ISH. Due to the low density of previously published sequences in the western Baltic Sea region, additional 24 samples from the brackish water fjord Præstø (PRA) (55°7'28"N, 12°2'27.15"E) and 24 samples from the inland freshwater lake Sjælsø (SJA) (55°52'50"N, 12°27'26"E) were included. All samples were collected during the spawning period, between 21 April and 24 May 2013. The samples were stored in ethanol in a -20°C freezer. DNA was extracted using Qiagen Blood and Tissue Kit according to the manufactures protocol (Qiagen Ltd, Crawley, UK). Polymerase chain reaction (PCR) amplification was done using forward primer HV2 and reverse primer CSB-D (Nesbø *et al.*, 1998a, b). PCRs were run for 30 cycles using an annealing temperature of 55°C. The resulting PCR products were purified and sequenced in both directions using the HV2 and CSB-D primers at Macrogen Europe. All sequences were aligned

Table I. - List of haplotype names for perch *Perca fluviatilis* in present and previous studies after the length trimming and removal of the repeat section.

Clade ID	Present study	Refseth *et al*., 1998	Nesbö *et al*., 1998b	Nesbö *et al*., 1999	Behrmann-Godel *et al*., 2004	Sruoga *et al*., 2007	Butkauskas *et al*., 2012
1-1				M, M1	M		
2-1				K, K1, K2			
3-1				J, J1			J
3-2				J2			
3-3							J3
4-1		K	K, M, N	C, C1, C2, C3, G1		C, C1, L1, G2	C, D
4-2						C4	
4-3							C5
5-1	5-1	C, H, I	C, L	E, E2, F, F1, F4, F6, F7	F	E, F, F1, F2, F7, F8	F, H, L4
5-2				F5	F5		
5-3	5-3						
5-4	5-4						
6-1	6-1	A, D, G, J	A, D, O	A, A2, A6, A7, A8		A, A2, A7, L2	A, B, B4
6-2		F					
6-3		B		A1			
6-4		E					
6-5							B6
6-6							A6, B7
6-7							B5

and edited relative to a perch mtDNA reference sequence (NCBI, Acc. No: Y14724).

In addition, mtDNA haplotypes were reconstructed from 707 perch described in previous published studies (Nesbø *et al*., 1998a, b, 1999; Refseth *et al*., 1998; Behrmann-Godel *et al*., 2004; Sruoga *et al*., 2007; Butkauskas *et al*., 2012) (Tab. I). All sequences were trimmed to a uniform length covering all samples using Geneious (Version 6.15, created by Biomatters). Furthermore, following Nesbø *et al*. (1998b) the repeat-section corresponding to positions 109-144 in reference sequence Y14724 was deleted.

A haplotype network of all haplotypes was constructed using Geneious. Sample sites located geographically close were concatenated and the 65 sample sites were reduced to 28. Haplotype frequencies for all 28 European sampling sites were calculated using Arlequin (Excoffier and Lischner, 2010), and were used to create a map of clade distributions using ArcMap V. 10.1 (ESRI, Redlands, USA).

RESULTS

Hatching experiment

Salinity measurements at the egg sampling site of ISH, ranged between 7 and 10 with an average of 8‰ throughout the spawning period. In the *in vivo* experiment, the larvae hatched successfully when the eggs were exposed to 4, 7, 10 and 12‰ water, in 75, 63, 88 and 63% of the samples, respectively. Egg samples that did not hatch were infected by fungus. The Fisher's Exact Test did not show significant difference in the hatching success between any of the treatments ($p > 0.05$) (Tab. II). No deformities were observed among the hatched larvae.

Table II. - Hatching experiment on perch *Perca fluviatilis*. **A**: Number of replicates with successful hatching at each salinity (n = 8); **B**: P values from pairwise Fisher's Exact Test.

A

Salinity ‰	No. of hatched samples
4	6
7	5
10	7
12	5

B

Salinity ‰	4	7	10
4			
7	1		
10	1	0.57	
12	1	1	0.57

DNA

The trimmed DNA sequences had a length of 260 bp, and included 17 variable sites. The trimming and removal of the repeat section resulted in six clades and 19 haplotypes (Fig. 2). The data set had a haplotype diversity and nucle-

otide diversity of 0.723 and 0.0068, respectively, and from the distribution of haplotypes it was disclosed that diversity is lowest in Western Europe and highest in the Baltic Sea region and south-eastern Europe (Fig. 3) in accordance with previous studies (Nesbø *et al*., 1999). The perch from the present study mainly consisted of haplotype 5-1, dominating in Central and Western Europe, but also had genetic sequences similar to those found in the Baltic Sea region. This mixed composition of sequences belonging to both Western and Eastern clades was also found in the other local brackish water population PRA, whereas the freshwater population SJA only had sequences belonging to western European clades. There was a significant difference between the brackish water populations (ISH and PRA) and the fresh water population (SJA) (F_{ST}: 0.116 and 0.214, $p < 0.05$), but no significant difference between the two brackish water populations (F_{ST}: 0.021, $p > 0.05$).

DISCUSSION

The results of the present study show that perch *Perca fluviatilis* eggs are able to hatch at salinities considerably higher than previously documented. If the high salinity tolerance for egg hatching is an inherit trait of European perch, the lower egg salinity tolerance (7‰) reported by Klinkhardt and Winkler (1989) might have been downward biased by their high incubation at temperature (18-20°C), which is known to decrease the hatching success of perch eggs (Guma'a 1978).

Alternatively, the higher salinity tolerance of perch eggs in the present study, compared to Klinkhardt and Winkler (1989), could be explained by intraspecific variability in salinity tolerance of perch eggs derived from either a phenotypic response or genetic differences. Such variation in salinity tolerance between populations have previously been demonstrated for many species of fish, including stenohaline freshwater teleosts, euryhaline teleosts and stenohaline saltwater teleosts (Vetemaa and Saat, 1996). Although mtDNA diversity is unlikely to be directly associated with salinity tolerance, the genetic diversities of the brackish water populations were significant different from the freshwater population, indicating that a genetic correlation with salinity tolerance could exist. Similar adaptive indications are described for pike (*Esox lucius*), another brackish water fish in the western Baltic Sea (Larsen *et al*., 2005; Jørgensen *et al*., 2010). Studies targeting the interspecific variation in salinity tolerance in perch and possible links to genetic markers are obvious topics for the future studies.

Other sensitive stages in the perch life cycle (*e.g*. fertilization, salinity tolerance of larvae) than egg hatching could be limiting factors for successful recruitment in brackish water. The growth of perch fry has been shown to decline with salinities above 4‰ (Overton *et al*., 2008; Tibblin *et al*., 2012), and generally, perch larvae have a natural high mortality within the first 14 days after hatching (Bein and Ribi, 1994; Wang and Eckmann, 1994). Nevertheless, the egg hatching results of the present study and successful rearing of these larvae at salinities of 10 and 12‰ at Den Blå Planet National Aquarium Denmark (pers. obs. Peter Gravlund), suggest that successful recruitment of perch takes place in at least one brackish water spawning site in the western Baltic Sea, as indicated by Skovrind *et al*. (2013).

Our results indicate that coastal spawning areas might be overlooked in the western Baltic Sea. Additional spawning areas would possibly be located close to stream deltas in places where other important factors, such as wave protection and spawning substrate (Snickars *et al*., 2010), are also present. Further identification of marine spawning sites of perch is important for management of coastal perch populations, highly valuable to the local society, recreationally and economically.

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